POLYDORA COMMENSALIS ANDREWS—LARVAL DEVELOPMENT AND OBSERVATIONS ON ADULTS [1]

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Although *Polydora commensalis* is often present in the shells of hermit crabs, many aspects of its life-cycle and biology have been overlooked. The larval stages have been incompletely known and there also is confusion as to the mode of fertilization.

The aims of this paper are (1) to describe the larval development of *P. commensalis* so that it might be recognized in waters where it has heretofore been overlooked or confused with other species, and (2) to investigate problems surrounding the annelid's habitat and method of reproduction.

Materials and Methods

Since a major aim of this investigation was to describe morphologically the larval development of *Polydora commensalis*, large numbers of the hermit crab, *Eupagurus pollicaris* Say, were obtained. All hermit crabs used in this study were collected in Noank Harbor (U.S.C. & G.S. Chart No. 358).

One hundred and two shells of hermit crabs were opened from November, 1962, to September, 1963, in search of *P. commensalis* egg strings. The four egg strings found provided fertilized eggs and young larvae for laboratory studies.

Stender dishes containing sea water which had been filtered through a Millipore filter, using pads with a porosity of 47 μ (Millipore Filter Corp., Bedford, Massachusetts), were used as rearing vessels. These vessels were immersed in a water bath of running sea water. Sea water in these vessels was changed three times a week. Liver powder was used as a source of food and a freshly prepared suspension was added at the time of each water change (Howie, 1958).

Larvae were also obtained in qualitative plankton tows, using a No. 10 net. Plankton tows were taken on the average of once weekly in front of the laboratory from November, 1962, through December, 1963. Larvae from this source were maintained in the same way as those reared from fertilized eggs.

Descriptions of laboratory-reared larvae and larvae collected from the plankton were made. Larvae were examined in either a hanging drop or under Saran Wrap (Dean and Hatfield, 1963). Larvae of various stages were photographed with a Polaroid camera mounted on a phase microscope. All drawings except

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Figure 1 were made from the photographs with the aid of a camera lucida or projector. Figure 1 was drawn from life, using a camera lucida. Larvae were returned unharmed to rearing vessels, following examination.

I. Observations on Adults

a. Distribution

Polydora commensalis was first reported as being present in shells of *Nassarius obsoletus* Say (= *Ilyanassa obsoleta*) inhabited by the hermit crab, *Eupagurus longicarpus* Say, at Beaufort, North Carolina (Andrews, 1891). Andrews also mentions finding this commensal annelid in association with *Eupagurus pollicaris*.

A more recent study reports that this spionid is present along the east coast of Canada, in the shells of *Nassarius obsoletus* occupied by *Eupagurus longicarpus* (Berkeley and Berkeley, 1956).

The author is unaware of any other publications reporting this annelid from the Atlantic coast of North America. However, specimens described in the present paper were found to be very common in various gastropod shells inhabited by *E. pollicaris* at Noank, Connecticut.

The reports of its presence on the west coast of North America are numerous. Berkeley and Berkeley (1936) reported it from Departure Bay, British Columbia, living in shells of *Thais lamellosa* Gmelin inhabited by *Pagurus granosimanus* (Stimpson). Its presence is also recorded in Nanoose Bay in the Nanaimo district, British Columbia (Berkeley, 1927) and from Southern California and Mazatlan, Mexico (Hartman, 1941).

It is further recorded from the North Japan Sea living in shells of *Natica* occupied by a species of *Eupagurus* (Annenkova, 1938). Thus, this annelid is found in several types of shells and in association with more than one species of hermit crab.

In the present study, *P. commensalis* was recorded from the following shells: *Lunatia heros* Say, *Polinices duplicata* Say, *Busycon canaliculatum* Linné and *Buccinum undatum* Linné. In all cases, the crab inhabiting these shells was *E. pollicaris*. Dr. David Dean (unpublished data) also recorded this annelid from Noank Harbor in a *Littorina littorea* Linné shell inhabited by *E. longicarpus*.

b. Habitat

The tubes of *Polydora commensalis* are constructed around the columella of shells by boring a deep furrow and roofing it over with a thin calcareous layer. These tubes are never visible unless the shell is cracked open and frequently extend from the lower part of the columella to the apex of the shell. Fertilized eggs or larvae were found within these tubes, along with an adult worm, during July and August of 1963.

Studies on reproduction, egg deposition, tube-building, etc., would be facilitated if tubes were visible. Therefore, the ability of adult *Polydora commensalis* to build visible tubes on shells and other substrates was tested. All shells used were cleaned by boiling in distilled water. Adult *P. commensalis* were capable of building calcareous tubes on some materials but not on others. All tubes were

exposed to view. The results are tabulated below:

Built Tube	Did Not Build Tube
Lunatia heros	*Nautilus pompilius*
Mercenaria mercenaria	Aragonite block
Spisula solidissima	Calcite chips
Thais lapillus	*Crepidula plana*
Littorina littorea	*Crassostrea virginica*
Busycon canaliculatum	*Mytilus edulis*
Polinices duplicata	*Anodonta* sp.

Calcareous tubes were constructed within approximately two weeks. A 3½- to 5-month period was allowed to elapse before a substrate was listed as not conducive to the construction of the calcareous tube of *P. commensalis*.

c. Reproduction

There has been much speculation as to how fertilization is accomplished in *Polydora commensalis*. This is due to reports that there is usually but one individual, always a female, per shell, and that the eggs are found within a concealed calcareous tube (Andrews, 1891; Berkeley and Berkeley, 1936). Individuals approximately 4 mm. in length have been noted by Andrews (1891) and Berkeley and Berkeley (1936). These authors were not able to determine the sex, but suggested that these small worms were males.

The results of this study are in vast disagreement with previous reports concerning number of worms per shell (Andrews, 1891; Berkeley and Berkeley, 1936). *P. commensalis* was found occurring in numbers of two or more per shell 56.7% of the time, and the number reached a total of seven in some instances. Also, these figures are on the conservative side, since it is very probable that some smaller specimens were overlooked. Often two or three of these worms would be found with their tubes side by side.

Furthermore, all *P. commensalis* found were not females. Sometimes only females were present in a shell and at times only males, while on other occasions members of both sexes were present. Sex was determined by presence of eggs or sperm. A total of 27 worms was observed with gametes throughout the winter, spring and summer months of 1963. Ten of these were females and 15 were males. On two occasions both eggs and sperm were found in a single worm. Gravid females ranged in length from 15 to 90 mm. with the average size being approximately 35 mm. Ripe males ranged in length from 3 to 17 mm. with the average length being approximately 12 mm. and the mode 15 mm.

Eggs were light yellow, measured approximately 120 μ in diameter, and were present from segment 14 onward.

All egg masses found within tubes contained fertilized eggs.

II. Larval Development

a. Development in the egg sac

Egg sacs and early development of *Polydora commensalis* Andrews were described by Andrews (1891). However, these stages are presented here, in order

to report additional data on ciliation, time of release of larvae to the plankton and other details.

Fertilized eggs and young larval stages are found in the adult tube within partitioned transparent cases (Fig. 1). Approximately 48 hours are required for fertilized eggs to develop into trochophores. At this stage, the beginning of a prototroch is present as two ciliated antero-ventral swellings. A poorly developed telotroch, situated postero-ventrally and laterally, is present as four patches composed of approximately two cilia per patch. The precursor to the vestibule appears anteriorly as a ventral ciliated depression. Neither an apical tuft nor dorsal ciliation are present. Although most trochophores possess two eyes, some specimens are totally lacking in this respect. This variation in number of eyes is evidenced in older larval stages as well. The most outstanding feature of the trochophore is the large yolk mass which comprises approximately 80% of the total body size.

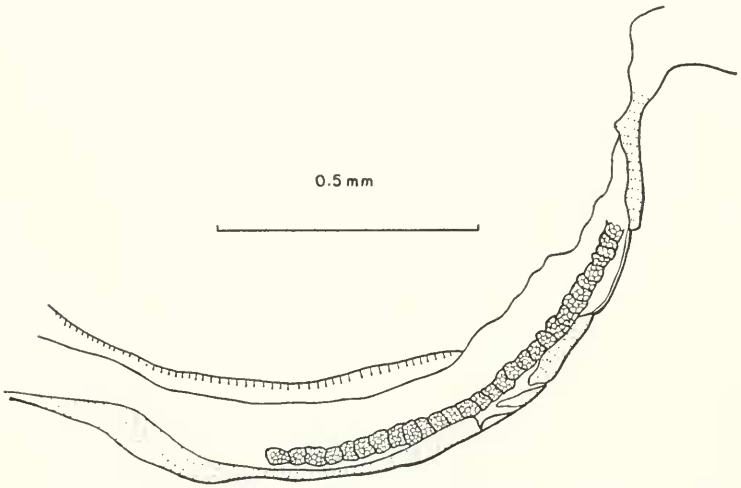

FIGURE 1. Egg string found within adult *P. commensalis* tube. The roof of the calcareous tube was broken in order to expose the eggs. The remnants of the tube are stippled in this figure.

About 24 hours are required for trochophores to advance to 3-segment larvae. At this stage, capillary serrate swimming setae are present on all segments (Fig. 2). A distinct prototroch and telotroch are present, neither of which extends across the dorsal side. The yellow-brown gut is still very yolky, and four eyes are now in evidence. Neither gastrotrochs nor nototrochs have yet appeared.

Two to three days later the larvae have added two achaetigerous segments and become very active (Fig. 3). The capillary notosetae have lengthened considerably and the development of the ciliation makes the larvae very adept swimmers by the 5-segment stage. A short capillary neuroseta appears on setiger 3, marking the transition from a uniramous to a biramous condition. No neurosetae were observed on segments 1 or 2; nor were there either noto- or neurosetae on segments 4 or 5 at this stage. The cilia of the prototroch and telotroch, which extend across the ventral side, have become longer and more powerful. The telotroch is

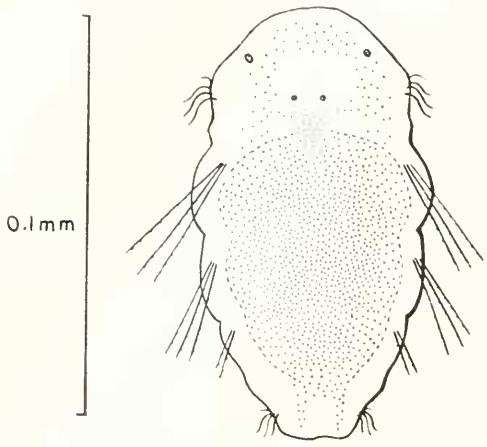

FIGURE 2. Three-segment *P. commensalis* larva. Dorsal view.

composed of distinct patches of cilia. Prominent gastrotrochs, extending across setiger 3 in six patches, and smaller nototrochs make their appearance at this stage. The nototrochs appear to be in six patches across the dorsal side of segments 3 and 4 and in two patches on segment 5. The V-shaped, ciliated vestibule

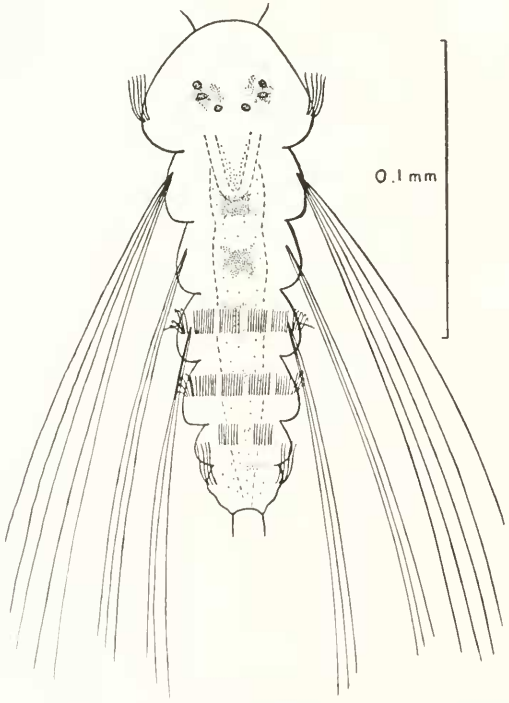

FIGURE 3. Five-segment *P. commensalis* larva. Dorsal view.

is now well developed and accentuated by yellow-brown pigment along its border. The larvae ingested liver powder for the first time at this stage. Perhaps the most striking development of the 5-segment larva is the appearance of a median dorsal row of ramified chromatophores. This is characteristic of larvae of all subsequent stages. Almost always these chromatophores are present on every segment, but occasionally they are absent on setigers 1 and 2. The black eyes number four to six and a chromatophore is present between the lateral and median eye on each side. The pygidium assumes a brownish hue and two small anal sensory cilia can be seen projecting from it.

Andrews (1891) suggested that the larvae leave the egg sacs at this stage. It was determined that this was the case by using a method similar to that employed by Wilson (1928) with *Polydora ciliata* larvae. An adult *Polydora commensalis* was left in its calcareous tube with its unbroken egg sacs in a dish of filtered sea water. For the next five days larvae were continually liberated. Twice a day these larvae were collected, examined, and the adult worm put in a dish with fresh sea water. In all cases the collected larvae were at a typical 5-segment stage. Furthermore, the earliest larval stage collected in the plankton possessed five segments, which adds credence to the above results.

b. Development outside the egg sac

The pelagic larvae of *Polydora commensalis* were found in the plankton of the Mystic River Estuary from July to November. Egg strings were found in shells of hermit crabs on four separate occasions during the months of July and August, 1963. The following descriptions characterizing planktonic larvae are based upon examination of many larvae from the above sources. The general description of the pelagic larvae which follows precedes a more detailed description.

One of the most noticeable features of the pelagic larvae is their pigmentation. Planktonic larvae of all stages possess a median dorsal row of black ramified chromatophores on all segments, except occasionally on segments 1 and 2. As the larvae become older and reach the 12- to 16-segment stage, lateral unramified black chromatophores appear on the anterior aspects of each segment. The pigmentation of the vestibule deepens as the larvae develop. The pygidium also appears quite dark. The median row of chromatophores becomes more ramified and spreads across the dorsum in older larvae. The anterior rim of the rounded prostomium is also noticeably pigmented in older larvae. The above pigmentation results in an overall dark appearance of the larvae when viewed with the naked eye or under low power of a dissecting microscope. The only other pigmentation is the black of the eyes. The latter number from zero to six in various specimens, but six is the most prevalent number. On either side there is usually a black ramified chromatophore between the most lateral eye and the eye nearer the midline of the body. One specimen, reared from a fertilized egg to a 28-segment stage, lacked eyes and bore only a median prostomial chromatophore.

The other most obvious characteristic of these larvae is the large size they attain. Specimens surpassing 2 mm. in length are not uncommon.

These general characteristics easily separate the larvae of *P. commensalis* from those of all other spionids reported in the literature to date, except *Polydora hermaphroditica* Hannerz (Hannerz, 1956) and "*Polydora* A" (Gravely, 1909).

The descriptions of these larvae show great similarities to *P. commensalis*. The more detailed examination which follows is necessary, therefore, to avoid confusion.

In early pelagic stages all setae are capillary. Notosetae are much longer than neurosetae. The fifth setiger does not become modified with stout hooks, characteristic of the genus, until the larva has reached a considerable size. The precise setiger stage at which this modification occurs is variable. These hooks have been observed as minute setae beneath the integument as early as the 15-segment stage. Conversely, they have not been seen in some specimens of 19-segments. However, presence of hooks often is noted between the 18- and 19-segment stage. Associated with the appearance of these modified setae is the reduction in number of capillary

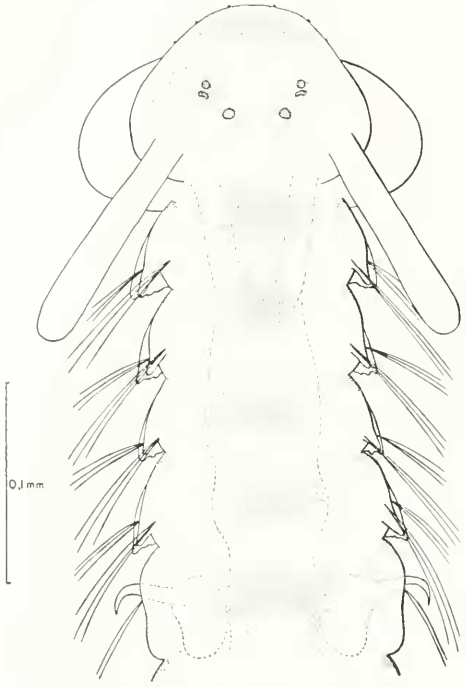

FIGURE 4. Anterior end of a 28-segment *P. commensalis* larva. Dorsal view; ciliation omitted.

neurosetae. The modified setae break through the integument at the 21- and 23-segment stage, and the capillary notosetae are lost.

Large glands, named "poches glanduleuses" by Claparède (Hannerz, 1956), become noticeable with the advent of the modified setae. These glands enlarge as the hooks increase in size (Fig. 4).

Shortly after the appearance of the modification of the fifth setiger, hooded bidentate crotchets appear in the neuropodia of the posterior segments. These are accompanied by bent capillary setae. On a few occasions the hooded crotchets were observed on larvae with as few as 18 segments. They were always present on larvae of 22 or more setigers and began on the eleventh to fourteenth setigers. All

segments have both dorsal and ventral cirri with the exception of the fifth. The ventral cirri are better developed (Fig. 5).

Ciliated swellings lateral to the vestibule become very apparent by the 12-setiger stage. These lateral lips continue to enlarge and in advanced larvae appear enormous when the mouth is wide open.

A prototroch runs across the ventral side of the lateral lips to either edge of the vestibule. It reaches the dorso-lateral edge of the lateral lips, but does not extend across the dorsal side. A minute prototroch is still observed as late as the 28-segment stage. The telotroch extends across the ventral side in patches. All larval stages exhibit a large dorsal gap. Neither a neurotroch nor ciliated pit has

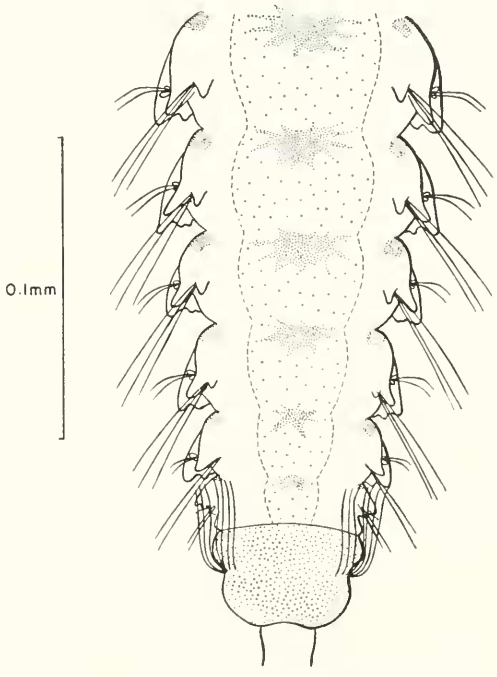

FIGURE 5. Posterior end of a 25-segment *P. commensalis* larva. Dorsal view; nototrochs omitted.

been observed at any stage. Prominent gastrotrochs are present in six to eight patches on segments 3, 5, 7, 10, 13, 15, 17, 19, 21, 23, 25, etc. Nototrochs are present in eight patches across the dorsum. The most lateral patch on each side is composed of "grasping cilia" (Wilson, 1928). Usually, nototrochs begin on segment 3 and are present on every segment thereafter. Occasionally, however, a small nototroch is present on segment 2.

Between the 9- and 10-setiger stage, small swellings, palpi anlage, are observed posterior to the prototroch and anterior to the first segment. These buds gradually increase in length, but remain rather small in relation to the body size, even in the oldest larval stages (Fig. 4). They are greatly reduced compared to other spionid larvae.

Branchial buds are never observed prior to the 22-segment stage. Even at the 28-segment stage they appear quite small, being present on setiger 6 and onward.

c. Metamorphosis and length of larval life

Unfortunately, experiments designed to induce metamorphosis were unsuccessful. Therefore, the length of larval life can be approximated only. Records were kept on the period of time it took for four larvae to develop from fertilized eggs to 27- to 29-segment stages. The results of four separate observations were 42 days, 44 days, 45 days and 38 days. This is an average of 42 days or approximately one and one-half months. After the 27-segment stage is reached, further development is very slow. For example, approximately 15 days were required for a larva to develop from a 27-segment to a 29-segment stage (Table I, specimen 1), whereas observations showed that a specimen might develop from a trochophore to a 14-segment stage in about the same length of time (Table I, specimen 4). The

TABLE I

Estimates of length of larval life of P. commensalis

Specimen no.	Date examined	No. segments	No. days after initial observation
1	July 9, 1963	Fertilized Egg	
	July 28, 1963	14	19
	Aug. 9, 1963	22 to 23	31
	Aug. 13, 1963	24 to 25	35
	Aug. 14, 1963	25	36
	Aug. 20, 1963	27	42
	Sept. 4, 1963	29	57
2	July 9, 1963	Fertilized Egg	
	July 11, 1963	Trochophore	2
	July 12, 1963	3	3
	July 15, 1963	5	6
	July 17, 1963	8	8
	July 29, 1963	14	20
	Aug. 1, 1963	18	23
	Aug. 5, 1963	19	27
	Aug. 10, 1963	23	32
	Aug. 15, 1963	25	37
	Aug. 22, 1963	27	44
3	July 11, 1963	Fertilized Egg	
	Aug. 2, 1963	12	22
	Aug. 25, 1963	28	45
4	July 15, 1963	Trochophore*	
	July 19, 1963	5	4
	July 22, 1963	6 to 7	7
	July 30, 1963	14	15
	Aug. 20, 1963	27	36

* Approximately 48 hours are needed to advance from the fertilized egg to the trochophore stage. Therefore, 2 days should be added to the figures in the column "No. days after initial observation" in order for these figures to correspond to the other 3 observations.

TABLE II

Length-frequency of P. commensalis *adults*

Length (mm.)	Frequency of occurrence	Cumulative
0–1	0	0
1.5–2	5	5
2.5–2	18	23
3.5–4	6	29
4.5–5	9	38
5.5–6	1	39
6.5–7	4	43
7.5–8	8	51
8.5–9	0	51
9.5–10	11	62
10.5–11	0	62
11.5–12	2	64
12.5–13	3	67
13.5–14	3	70
14.5–15	8	78
15.5–16	0	78
16.5–17	1	79
17.5–18	1	80
18.5–19	0	80
19.5–20	4	84
20.5–21	0	84
21.5–22	1	85
22.5–23	0	85
23.5–24	0	85
24.5–25	3	88
25.5–26	0	88
26.5–27	2	90
27.5–28	1	91
28.5–29	0	91
29.5–30	0	91
30.5–31	0	91
31.5–32	0	91
32.5–33	1	92
33.5–34	0	92
34.5–35	0	92
35.5–36	0	92
36.5–37	0	92
37.5–38	0	92
38.5–39	0	92
39.5–40	2	94
40.5–89.5	0	94
90 –90.5	1	95

Notes: The total number of worms collected from shells was 109. The total number of worms where measurements were taken was 95.

latest stage a larva attained in these experiments was 29-segments. After remaining at this stage unmetamorphosed for 21 days, it was preserved.

The length of larval life is probably shorter in nature. By the 22-setiger stage the larvae have acquired all the features of a young benthic worm. The fifth setiger has been modified, hooded crotchets have appeared and branchial anlage are present.

If one assumes larvae are capable of metamorphosing when these features have developed, then the larval life would be reduced to approximately one month (Table I, specimens 1 and 2).

d. Comparison of larvae of Polydora commensalis with Polydora hermaphroditica

The larvae of *Polydora hermaphroditica* (Hannerz, 1956) and "*Polydora* A" (Gravely, 1909) greatly resemble larvae of *Polydora commensalis*. "*Polydora* A" has been reported as identical to *P. hermaphroditica* (Hannerz, 1956).

Larvae of *Polydora hermaphroditica* are very similar to advanced larvae of *Polydora commensalis* in regard to pigmentation, size, ciliation and time of occurrence in the plankton. However, the latter has the following distinguishing characteristics. Branchial anlage are clearly evident from segment 6 onwards. The dorsal median row of ramified chromatophores is present from segment 1 to the posterior end, except on occasion when they are absent on segments 1 and 2. Small unramified chromatophores are present laterally on the anterior side of each segment. They often continue to the posterior end, although at times are lacking in the last few segments. Bidentate hooded crotchets in the neuropods begin between segments 11 and 14, whereas they are found more anterior in *P. hermaphroditica*.

The above characters seem to be the most outstanding features by which to separate the two species. Although the author knows of no reports of the presence of *P. hermaphroditica* in American waters nor *P. commensalis* in European waters, it is important that specimens collected in the plankton be examined critically. It will be interesting to learn whether these species are more widely distributed than reported.

Discussion

Polydora commensalis larvae exhibit typical polydorid characters in regard to morphology, deposition of eggs within the adult tube and planktotrophic pelagic larvae. Inconclusive data indicate that copulation, also typical of the genus, occurs. *Polydora commensalis* has a short period of brood protection followed by a long pelagic life. This species can delay metamorphosis, as shown by one specimen which remained unmetamorphosed at the 29-segment stage for 21 days. Both a long pelagic life and the ability to delay metamorphosis would be advantageous to this species in finding its host.

Adults of *Polydora commensalis* are found in several types of shells and in association with more than one species of hermit crab. This distribution indicates that the commensal relationship is not highly specific. However, one must hesitate in referring to *Polydora commensalis* as a facultative commensal, since there are no reports of adults living in a free state. Usually, when a number of different species may act as host for a commensal, the factors which cement the relationship are quite general in nature (Dales, 1957). In the case presently being discussed, it would appear that the main factors are food and shelter. Furthermore, the host is active and, thus, the more passive annelid obtains benefit by the avoidance of stagnation. The inside of the hermit shell is kept well aerated with fresh sea water. This is accomplished by the current of water from the branchial chamber of the crab, aided by the beating of the pleopods (Jackson, 1913).

The general nature of the relationship was further evidenced by the ability of

P. commensalis to form tubes on various shells which could never be occupied by hermit crabs, *i.e.*, lamellibranch shells. All of the above, plus the fact that this annelid is reported from both sides of the globe, lead to the speculation that *P. commensalis* may be more widely distributed than reported.

During the studies on the reproduction of *P. commensalis* sufficient evidence was collected to speculate that fertilization is accomplished by copulation. In summary, the data tabulated below support this theory.

1. Both males and females are often present in the same shell with their tubes in close proximity.
2. The worms are capable of extending far out of their tubes, thus allowing the sexes to meet and copulation to take place.
3. On occasion, worms in the size range of females are found to contain sperm as well as eggs, indicating copulation had taken place.
4. All egg masses found contained fertilized eggs.

Although the occurrence of several *P. commensalis* of both sexes in one shell seems to have been overlooked previously, the occasional presence of a minute individual approximately 4 mm. in length has been noted (Andrews, 1891; Berkeley and Berkeley, 1936). Andrews had speculated that these minute annelids were males, and hence there was an interesting case of sexual dimorphism in regard to size. However, neither Andrews nor Berkeley and Berkeley were successful in determining if this were the case. In this study, ripe males were found to average a length of 12 mm. On only one occasion were sperm found in worms of 1.5 to 5 mm. in length, though a total of 38 worms were found in this size range (Table II).

Summary

1. *Polydora commensalis* larvae were found in the plankton from July to November, 1963, and fertilized eggs were found in the tubes of adults in July and August.

2. Fertilized eggs develop into 5-segment larvae within 5 to 7 days, at which stage they are liberated to the plankton.

3. Ciliation, setation, pigmentation and other taxonomically important features are described for larvae from the trochophore to 29-segment stage. Planktonic larvae of all stages possess a dorsal median row of black ramified chromatophores. Advanced larvae may exceed 2 mm. in length. The pigmentation and large size attained are the most outstanding characteristics of *P. commensalis* larvae.

4. Due to the similarity between larvae of *P. commensalis* and *P. hermaphroditica*, a comparison of the two is given.

5. The length of larval life of *P. commensalis* is estimated to be between one and one and a half months.

6. Data on distribution, habitat and reproduction are reported. It is suggested that this annelid is more widely distributed than reported, and that fertilization is accomplished by copulation.

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